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Emerging Neurophysiological Specialization for Letter Strings

Urs Maurer, Silvia Brem, Kerstin Bucher, and Daniel Brandeis

Abstract

■ In adult readers, printed words and other letter strings activate specialized visual functions within 200 msec, as evident from neurophysiological recordings of brain activity. These fast, specialized responses to letter strings are thought to develop through plastic changes in the visual system. However, it is unknown whether this specialization emerges only with the onset of word reading, or represents a precursor of literacy. We compared 6-year-old kindergarten children who could not yet read words to adult readers. Both age groups detected immediate repetitions of visually presented words, pseudo-words, symbol strings, and pictures during event-related potential (ERP) mapping. Maps from seven corresponding ERP segments in children and adults were analyzed regarding fast (<250 msec) and slow (>300 msec) specialization for letter strings. Adults reliably differentiated words through increased

fast (<150 msec) occipito-temporal N1 activity from symbols. Children showed a later, more mid-occipital N1 with marginal word-symbol differences, which were absent in those children with low letter knowledge. Children with high letter knowledge showed some fast sensitivity to letter strings, which was confined to right occipito-temporal sites, unlike the stronger adult N1 specialization. This suggests that a critical degree of early literacy induces some immature, but fast, specialization for letter strings before word reading becomes possible. Children also differentiated words from symbols in later segments through increased right occipito-temporal negativity for words. This slow specialization for letter strings was not modulated by letter knowledge and was absent in adults, possibly reflecting a visual precursor of literacy due to visual familiarity with letter strings. ■

INTRODUCTION

Learning to read represents a major landmark in normal child development. Reading must be explicitly taught, as it does not develop “automatically” in preschoolers despite abundant exposure to printed words in their everyday environment. With further practice, reading skills are refined and continue to improve until adolescence. Neurophysiological studies on normal reading in adults have identified fast visual brain processes specialized for processing letter strings (i.e., words and other letter strings). Because reading skills are not innate, this specialization implies a major plastic reorganization of the brain during normal child development. The development of this fast visual specialization for letter strings has yet to be studied. Although the most obvious hypothesis is that it accompanies or follows word reading skills, it may also develop before instruction due to early letter knowledge, or even more general visual familiarity acquired by frequent exposure to printed words.

Rapid (N1 Component) Visual Specialization for Letter Strings

N1 Time Range

Reading has long been known to depend on specialized visual areas interacting with classical visual and language regions, evidenced by resultant selective alexia or word “blindness” arising from visual lesions (Cohen, Martindale, et al., 2003; Dejerine, 1892). Neurophysiological studies have since demonstrated that these visual regions play an active role in the initial (<250 msec) phase of specialized processing of letter strings. Consistent results have been obtained across different neurophysiological methods, task conditions, and languages. Intracranial recordings, with their excellent temporal and spatial resolution, provided the most direct evidence for specialization for letter strings, although the recordings were limited to patients with intractable seizures and only a small set of inferior-temporal regions were tested. In a study by Nobre, Allison, and McCarthy (1998), letter strings evoked negative peaks after 140–220 msec in the bilateral posterior fusiform gyrus. This intracranial N200 was absent for checkerboards, unaffected by attention (Nobre et al., 1998), and preceded the more anterior temporal P400 activation reflecting lexical and semantic features (Nobre, Allison,

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& McCarthy, 1994). This is consistent with word-related activation progressing from posterior to anterior temporal structures within the first 400 msec (Fernandez et al., 2001). Word- and face-specific N200 sites were found nearby but were not overlapping (Nobre et al., 1994), and half of the word-specific sites responded to faces with the opposite polarity (P200) and vice versa (Allison, Puce, & McCarthy, 2002). Mapping word-related brain activation at millisecond time resolution with scalp-recorded electric fields (event-related potential [ERP]) or magnetic fields (magneto-encephalogram [MEG]) reveals a corresponding transient N1¹ microstate (between about 120 and 240 msec) of large amplitude in a wide range of verbal or visual tasks.

N1 Topography

The electrical N1 topography is characterized by bilateral occipito-temporal negativity which is often left-lateralized (Brem et al., 2005; Rossion, Joyce, Cottrell, & Tarr, 2003; Vitacco, Brandeis, Pascual-Marqui, & Martin, 2002; Brandeis, Lehmann, Michel, & Mingrone, 1995; Dehaene, 1995), and by a central positivity (P150; Schendan, Ganis, & Kutas, 1998). This topography results in left-lateralized basal occipito-temporal gradient and source solutions (Rossion, Joyce, et al., 2003; Khateb, Michel, et al., 2001; Michel et al., 2001; Brandeis, Lehmann, et al., 1995) matching the corresponding MEG source solutions (Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). The left lateralization is sometimes confined to a distinct microstate after 200 msec (Khateb, Pegna, Michel, Landis, & Annoni, 2002; Khateb, Michel, et al., 2001; Michel et al., 2001; Cohen, Dehaene, et al., 2000), and distinguishes the word N1 from a more right-lateralized face N1 (Taylor, Batty, & Itier, 2004; Rossion, Joyce, et al., 2003; Pizzagalli et al., 2002).

N1 Sensitivity

The N1 is characterized by coarse prelexical sensitivity to letter strings. It strongly differs between letter and symbol strings, whereas the preceding visual P1 at about 100 msec is similar for these stimulus categories (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Tarkiainen et al., 1999; Schendan et al., 1998). The N1 is consistently larger for letter strings and pseudofont strings than for visually matched word scrambles, symbol, or icon strings in both ERP (Bentin et al., 1999; Schendan et al., 1998; Zhang, Begleiter, Porjesz, & Litke, 1997) and MEG (Tarkiainen et al., 1999) studies. In dyslexia, fewer N1 sources respond specifically to letter strings (Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1999; Salmelin, Service, Kiesila, Uutela, & Salonen, 1996), although the overall N1 response to

words is not reduced (Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000; Brandeis, Vitacco, & Steinhausen, 1994). This sensitivity of the N1 to letter strings appears to be largely automatic, as it is also obtained for implicit reading during detection of immediate repetitions or visual features (Bentin et al., 1999; Schendan et al., 1998). The effect appears specific to strings of letters, because single letters do not evoke larger N1 amplitudes than do shapes (Pernet et al., 2003; Gros, Doyon, Rioual, & Celsis, 2002). The lexical sensitivity of the N1 is less pronounced and more task-dependent. In implicit reading tasks, the N1 is usually indistinguishable for all types of letter and pseudofont strings (Bentin et al., 1999; Schendan et al., 1998), although subtle word-consonant string differences have been reported (Compton, Grossenbacher, Posner, & Tucker, 1991). Sensitivity to lexical differences is more common in explicit linguistic tasks, where the N1 is typically larger for consonant strings than for words (Bentin et al., 1999; McCandliss, Posner, & Givon, 1997). In contrast, the N1 is typically unaffected by lexical, semantic, linguistic, and repetition status which all modulate later components (Khateb, Pegna, et al., 2002; Kim, Kim, & Kwon, 2001; Bentin et al., 1999; Brandeis, Lehmann, et al., 1995; Dehaene, 1995; Nobre & McCarthy, 1994). However, there are notable exceptions, for example, an increased N1 is often observed for low-frequency versus high-frequency words (Hauk & Pulvermuller, 2004; Sereno, Brewer, & O'Donnell, 2003; Sereno, Rayner, & Posner, 1998) and for repeated versus novel words (Curran, Tanaka, & Weiskopf, 2002). Furthermore, topographic N1 differences between word classes also suggest an influence of higher-level processing on the N1 (Skrandies & Chiu, 2003; Skrandies, 1998; Koenig & Lehmann, 1996). Taken together, the results indicate that linguistic processing can overlap with the N1.

Thus, the N1 to letter strings seems to reflect fast, coarse, and partly automatized perceptual categorization within a domain of expertise, analogous to the N1 for faces (Rossion, Joyce, et al., 2003; Schendan et al., 1998). The distinct N1 topographies for words and faces appear to reflect the different domains, and their high amplitudes reflect the degree of cumulative domain-specific expertise. Although most adults share expertise for words and faces, the N1 also reflects individual perceptual expertise and plasticity in adults. Accordingly, N1 amplitudes are also enlarged for categories of personal perceptual expertise such as birds or dogs (Tanaka & Curran, 2001), and increase for nonsense shapes after perceptual training (Brem et al., 2005; Curran et al., 2002; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). The lack of N1 changes to pseudowords despite 5 weeks of lexical and semantic training in an artificial pseudoword language (McCandliss, Posner, et al., 1997) provides further support that the N1 reflects coarse perceptual rather than lexical and semantic processes.

Metabolic Localization of Visual Specialization for Letter Strings

Visual Word Form Area

Metabolic neuroimaging (PET, fMRI) has revealed consistent word-related activation in the visual extrastriate (Petersen, Fox, Posner, Mintun, & Raichle, 1988) and inferior posterior temporal regions during reading. This also holds for feature or repetition detection tasks which involve only implicit reading (Tagamets, Novick, Chalmers, & Friedman, 2000; Price, Wise, & Frackowiak, 1996). Increased activation near the left midfusiform gyrus for letter strings versus checkerboards (Cohen, Lehericy, et al., 2002), for Japanese character versus pseudofont strings (Fujimaki et al., 1999), for written versus spoken words (Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002), and for letter versus digit strings (Polk et al., 2002) suggests that this region is involved in visual word processing and has been termed the “visual word form area” (McCandliss, Cohen, & Dehaene, 2003; Cohen, Dehaene, et al., 2000). Activation of this region appears to play a critical role in fluent reading, as it is consistently reduced in adult dyslexics across explicit and implicit reading tests (Brunswick, McCrory, Price, Frith, & Frith, 1999) and different languages (Paulesu et al., 2001). Similarly, patients with pure alexia show consistent damage in this region and appear to activate the right-hemisphere homologue during slower letter-by-letter reading (Cohen, Martinaud, et al., 2003).

Letter-String-Specific Network

Although the left midfusiform gyrus seems to play an important role in visual word processing, it is part of a larger bilateral infero-posterior network with a similar degree of activation but with differing distributions for consonant or nonletter strings (Cohen, Martinaud, et al., 2003; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003; Tagamets et al., 2000). Accordingly, Tagamets et al. (2000) found that more wordlike stimuli (words vs. pseudo-words vs. consonant-strings vs. false-fonts) did not elicit stronger left fusiform activation, but increased the left lateralization of the bilateral fusiform network due to reduced activation of its right homologue (Tagamets et al., 2000). This suggests that the fusiform network may code more general aspects of visual expertise for wordlike strings, and does not represent an isolated word-specific module (for reviews, see McCandliss, Cohen, et al., 2003; Price & Devlin, 2003).

EEG-fMRI Relation

Although the metabolic left fusiform activation is consistent with neuroelectric and magnetic word N1 source

solution, the temporal resolution of fMRI and PET data is too low to differentiate fast and slow specialization for letter strings and to exclude contributions from later, sustained, or re-entrant activation of the same region (Dale et al., 2000; Nobre et al., 1998). Case studies provide more direct support that left midfusiform gyrus activation contributes directly to the word N1. Such studies have established strong agreement between left fusiform BOLD activation and N1 sources within individuals performing the same task in both imaging modalities (Cohen, Dehaene, et al., 2000; Dale et al., 2000).

Development of Visual Specialization for Letter Strings

Precursors of Reading

Extensive behavioral studies have identified a major role played by early phonological skills and letter knowledge in subsequent reading acquisition (Torgesen, Wagner, & Rashotte, 1994; Bradley & Bryant, 1983). Similar results have been obtained for German-speaking children, who learn to read considerably later (after age 6) than their English-speaking peers (Schneider, Roth, Küspert, & Ennemoser, 1998; Näslund & Schneider, 1996; Wimmer, Landerl, Linortner, & Hummer, 1991). In contrast, little empirical support has been obtained for an initial visual, logographic phase of whole word recognition in children with low letter knowledge (Treiman, Sotak, & Bowman, 2001).

Developmental ERP Studies

The development of visual N1 specialization for words over consonant strings (Compton et al., 1991) was examined in an implicit reading task with children (Posner & McCandliss, 2000). No N1 specialization was found in preliterate children or in young (7- and 10-year-old) readers. The visual word N1 (but not its specialization for letter strings) was also examined in systematic ERP studies on the development of visual word processing from beginning to skilled readers (Grossi, Coch, Coffey-Corina, Holcomb, & Neville, 2001; Taylor & Smith, 1995; Holcomb, Coffey, & Neville, 1992). The topographic changes specific to the semantic (Holcomb et al., 1992) and phonological (Grossi et al., 2001) processes affected later components (>250 msec) and indicated continued reorganization of language processing systems until late adolescence. The developmental decreases of N1 amplitude and latency (Grossi et al., 2001; Holcomb et al., 1992) paralleled changes found for most later ERP components, were independent of task condition, and may reflect nonspecific effects of maturation and automatization. Developmental topographic changes, which are more likely to reflect visual special-

ization, appeared less prominent in the N1 than in later components (Grossi et al., 2001; Holcomb et al., 1992). However, some topographic effects may have gone undetected in these studies due to separate analyses of anterior and occipital sites, and because posterior temporal regions were not covered. These regions are known to yield the largest word N1 in adults (Rossion, Joyce, et al., 2003; Brandeis, Lehmann, et al., 1995; Nobre & McCarthy, 1994), and a sizable N1 (although still smaller than at occipital sites) in 11-year-old (Brandeis, Vitacco, et al., 1994) and in 13-year-old (Hepworth, Rovet, & Taylor, 2001) children.

Developmental ERP studies thus reveal prominent maturation with faster and more automatic processing across all processing stages, and considerable specialization of phonological and semantic processing reflected by later ERP effects after 250 msec beyond age 15. They also indicate that the subtle effects of words versus consonant strings (orthographic regularity) on fast visual word processing emerge after the first 5 years of literacy instruction. However, they leave open how early the amplitude and topography of the N1 starts to reflect visual specialization for letter strings, and whether an early, coarse specialization becomes refined with further experience and development. Such a developmental pattern has been demonstrated for the face N1, which emerges as an “infant N1” with coarse sensitivity for human faces in the first year of life (de Haan, Pascalis, & Johnson, 2002), but does not reach its adult topography and sensitivity before age 14 (Taylor, Edmonds, McCarthy, & Allison, 2001).

Developmental fMRI Studies

Developmental fMRI studies indicate that consistent left-lateralized fusiform and temporal activations are already present in 5- to 7-year-old beginning readers during silent reading (Gaillard, Balsamo, Ibrahim, Sachs, & Xu, 2003). However, despite similarities, marked age- and performance-related activation differences are found between adults and 9-year-old children in extrastriate and frontal regions during overt word reading (Schlaggar et al., 2002). Similarly, although most activated regions overlapped between 11-year-old children and adults and between orthographic, phonological, and semantic tasks, the children still had less bilateral fusiform, and stronger left-posterior temporal activation (Booth et al., 2001). Increasing left fusiform, as well as decreasing right fusiform, activation during phonological and semantic tasks also correlated with better reading skills in a larger developmental study of dyslexic and control children between the age of 8 and 18 (Shaywitz et al., 2002). In an implicit reading task, age (range 6–22 years) and reading skill also correlated with deactivation in right inferotemporal regions, but not with increased left fusiform cortex activation (Turkeltaub et al., 2003).

Developmental Origin

In conclusion, developmental ERP and fMRI studies of visual word processing demonstrate that basic features (components and localizations) of the adult posterior network specialized for processing visual words are already present in novice readers, but undergo further development as reading proficiency progresses. However, it is not known whether this holds true for children before they can read words, and the few ERP studies with preliterate children were not designed to detect N1 specialization. On theoretical grounds, researchers have suggested that this specialization may originate either with school-age learning (McCandliss & Noble, 2003; Polk et al., 2002), or may develop in very young children for iconographic word-recognition strategies (Turkeltaub et al., 2003). Our study was designed to empirically resolve this issue.

The Current Study: Goals, Rationale, and Working Hypotheses

Our goal was to characterize the emergence of coarse visual specialization for letter strings by focusing on the visual N1 before word reading is acquired. We studied kindergarten children who were unable to read words, using a repetition detection task with words, pseudowords, symbol strings, and pictures (Figure 1, similar to Brem et al., 2005; Helenius et al., 1999; Tarkiainen et al., 1999), and compared them to skilled adult readers. The task required only implicit reading, and the symbol strings were matched with words and pseudowords for basic visual stimulus properties to discern word-specific visual development from more general development. Although the word–symbol comparison allowed us to investigate coarse specialization for letter strings, including pseudoword and picture conditions enabled us to further confine this specialization. The late start of reading instruction in Swiss schools at the age of 7, combined with the lack of early literacy instruction in kindergarten, offers a unique opportunity to investigate neural plasticity induced by learning to read at a well-defined age, and with phonological and visual abilities already well developed.

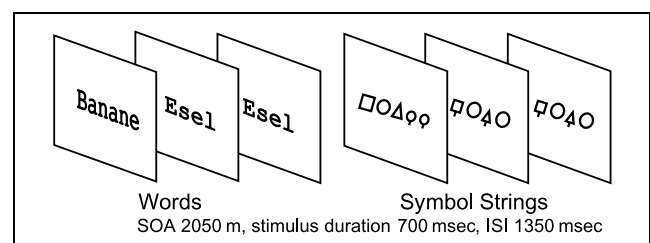


Figure 1. Word and symbol string stimuli (examples).

We focused on comparing children's and adults' visual word and symbol string processing. Temporal and spatial aspects of this specialization were examined using 43-channel ERP mapping and low-resolution electromagnetic tomography (LORETA) source localization. Adaptive segmentation was applied to identify quasi-stable map configurations of the ERP components (Lehmann & Skrandies, 1980). A critical point of our ERP analysis strategy is the differentiation between early (P1, N1) and late (P2, P3) components, and consequently, between fast (<250 msec) and slow (>300 msec) specialization for letter strings. The emergence of word–symbol differences (factor “wordlike” in the analyses) over time segments and with literacy skills was analyzed using measures of map strength (Global Field Power [GFP]), map topography (positive and negative 3-D centroids), and bootstrapping statistics of segment map differences. These measures allow comprehensive multichannel ERP analyses (e.g., Maurer, Bucher, Brem, & Brandeis, 2003a, Maurer, Bucher, Brem, & Brandeis, 2003b; Khateb, Pegna, et al., 2002; Khateb, Michel, et al., 2001; Michel et al., 2001; Brandeis, van Leeuwen, et al., 1998; Strik, Fallgatter, Brandeis, & Pascual-Marqui, 1998; Brandeis, Lehmann, et al., 1995; Brandeis, Vitacco, et al., 1994). To ease comparison with previous work, we included conventional N1 amplitude and lateralization analyses, occipito-temporal ERP waveshapes, and N1 peak maps for the four stimulus conditions with *t*-curves and *t*-maps for planned contrasts, and *t*-maps of all word–symbol segment differences.

We expected to replicate a reliable word–symbol string difference in the N1 of skilled adult readers indicating fast specialization for letter strings. For the critical N1 difference between words and symbols in children who could not yet read words, we considered two competing hypotheses.

1. If the N1 reflects efficient orthographic coding of letter strings, which develops only after learning to read, we would observe no N1 word–symbol difference in nonreading children. We considered this as the most obvious hypothesis. The lack of an N1 specialization for isolated letters in adults (see above) suggests that this should hold regardless of letter knowledge.

2. If the N1 reflects different visual aspects of processing letter strings in children than in adults, we would observe some N1 word–symbol differences in children. Such differences were expected to be less consistent and to show a different topography from adults, probably reflecting expertise limited to isolated letter knowledge and visual familiarity with letter strings. Such N1 differences would not reflect automatized orthographic coding, but could be tuned later by the intensive reading training and develop into the N1 difference of skilled readers.

We expected that adults, but not children, would perform better with words than with symbol strings, because

only the adults could implicitly read the words and efficiently code them to detect repetitions. However, we could not rule out the possibility that in illiterate children, familiarity effects for individual letters would lead to a performance benefit for words as compared to symbols.

We also predicted that the later ERP components would show word–symbol differences reflecting the differing strategies and attentional demands (reading vs. feature detection) of repetition detection for adult readers, but not for illiterate children. We hypothesized that the children might instead display a different pattern of late word–symbol string differences, reflecting their letter knowledge and visual familiarity with letter strings.

No word–symbol string differences were expected for the visual P1 because the stimuli were matched for basic visual properties.

In the planned comparisons, word–pseudoword differences were not expected at the performance level nor at the N1 level, which tends to be insensitive to lexicality. For the symbol–picture comparison, we expected similar, small N1 components, because both adults and children lack visual expertise for our symbols and pictures. Behaviorally, however, we expected a performance advantage for pictures due to more efficient (probably semantic) processing. For the word–picture comparison, we expected the same N1 differences as in the word–symbol comparison due to specialization for letter strings (strong for adults, absent for children). Behaviorally, we expected similar (good) detection performance for both words and pictures in adults, but poorer performance for words in children due to inefficient coding of letter strings.

RESULTS

Behavior

Adults detected repetitions with a greater accuracy than children [Age group, $F(1,34) = 94.66, p < .001$]. Table 1

Table 1. Behavioral Results

	<i>Words</i>	<i>Symbols</i>	<i>Pseudowords</i>	<i>Pictures</i>
Children RT (msec)	987	908	1111	845
Children misses (%)	48.6	44.8	53.7	24.0
Children false alarms (%)	7.5	9.9	8.7	1.6
Adults RT (msec)	543	556	557	519
Adults misses (%)	0.6	9.6	2.5	1.2
Adults false alarms (%)	0.0	1.5	0.0	0.3

shows the difficulty of the task for children. Although they missed nearly 50% of the repeated strings, their low false alarm rate (under 10%) clearly indicates that they were not simply guessing. The group difference was larger for words than for symbols [Age group \times Wordlike, $F(1,34) = 7.49, p < .01$]. Post hoc tests revealed that children missed word and symbol targets at an equal rate [$t(22) = 0.66, p = ns$], whereas adults missed fewer words than symbols [$t(12) = -3.28, p < .01$].

Children had longer reaction times than adults [Age group, $F(1,33) = 60.60, p < .001$], and this tended to be more pronounced for words than for symbols [Age group \times Wordlike, $F(1,33) = 3.40, p < .1$]. Post hoc analyses revealed that children had longer reaction times for words than for symbols [$t(21) = 2.33, p < .05$], whereas reaction times in adults were similar for both stimulus conditions [$t(12) = -0.43, p = ns$].

The additional planned comparisons between words and pseudowords, and between symbols and pictures, revealed similar results for children and adults. Both age groups showed no accuracy differences between pseudoword and word targets [children: $t(22) = -1.01, p = ns$; adults: $t(12) = -1.39, p = ns$], but missed fewer picture targets than symbol targets [children: $t(22) = -3.59, p < .01$; adults: $t(12) = -2.75, p < .05$]. Although adults' reaction time did not differ between words and pseudowords [$t(12) = -0.65, p = ns$], children tended to respond more slowly to pseudowords [$t(21) = -1.96, p < .1$]. No reaction time differences between symbols and pictures were observed [children: $t(21) = -1.19, p = ns$; adults: $t(12) = 1.24, p = ns$]. In contrast, the planned comparison between words and pictures revealed differences in children and adults: children were more accurate [$t(22) = 5.71, p < .001$] and faster [$t(22) = 3.17, p < .01$] in detecting picture targets than word targets, whereas adults showed similar performance [accuracy: $t(12) = -0.56, p = ns$; reaction time: $t(12) = 1.38, p = ns$].

ERP Segmentation

To compare different stages of information processing, the ERPs were adaptively segmented. This resulted in seven segments (S1 to S7) in both age groups, all with longer latencies and more GFP in children than in adults (Figure 2). Although GFP essentially decreased in strength from S1 (P1) to S7 for children, the S2 (N1) to words and S4 (P300) to symbols showed most GFP in adults. Whereas the first two segments (P1, N1) index fast processing/specialization (<250 msec), the remaining segments index slow processing/specialization (>300 msec).

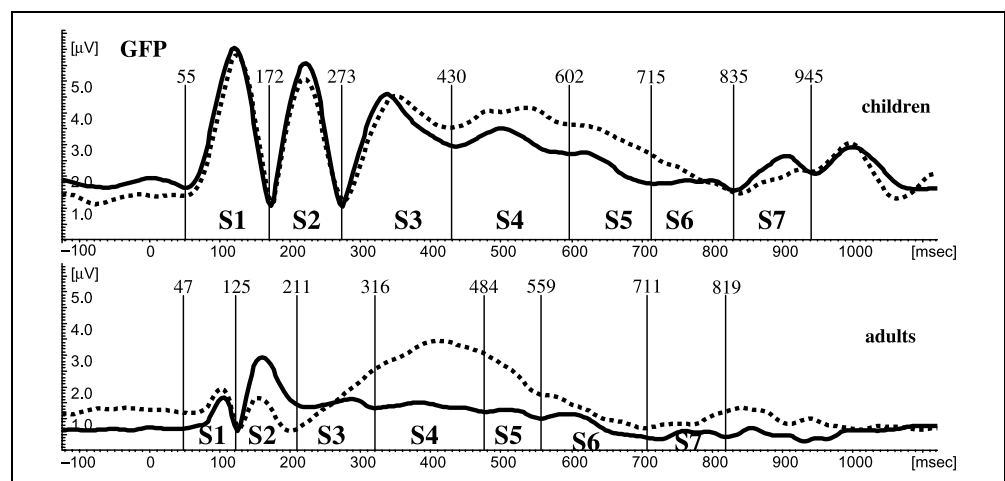
Global ERP Comparisons for All Segments

Two repeated-measures multivariate analyses of variance (MANOVAs) were used to analyze global ERP map descriptors "map strength" and "map topography" regarding differences between adults' and children's (factor "age group") specialized processing of letter strings (word-symbol difference, factor "wordlike") unfolding over the seven segments (factor "segment"). GFP was used to estimate the global strength or amplitudes of the segment maps. To measure map topography, separate centroids (centers of gravity) were computed for positive and negative values (factor "polarity") in a 3-dimensional space (x -, y -, and z -axes, treated as multivariate dependent measures). We use the term "centroid distribution" to describe differential effects on positive and negative centroids (statistical interaction with "polarity"), and "centroid mean location" for parallel effects on positive and negative centroids (no interaction with "polarity").

Map Strength (GFP)

Between-group comparisons. For all participants, symbols evoked greater GFP than words [Wordlike,

Figure 2. Segmentation of the ERPs. Segmentation for children (top) and adults (bottom) based on GFP curves to words (solid line) and symbol strings (dotted line). The vertical lines between the segments (S1–S7) depict segment borders with border latency (msec). Longer latencies, larger amplitudes, and only minor differences between words and symbol strings are evident in children as compared to adults.



$F(1,34) = 13.09, p < .001$], especially in Segments 4 to 6, whereas in Segment 2 words had greater GFP than symbols [Wordlike \times Segment, $F(6,29) = 7.94, p < .001$]. This pattern tended to differ between children and adults [Wordlike \times Segment \times Age group, $F(6,26) = 2.12, p < .1$], especially in Segments 1, 3, and 7. Children's ERP maps had increased GFP compared to adults' [Age group, $F(1,34) = 71.77, p < .001$]. This difference was present in each segment, but was most prominent in Segment 1 (P1) and least prominent in Segment 5 [Age group \times Segment, $F(6,29) = 2.52, p < .05$]. In addition, the seven segments had different GFP, with highest values in Segment 4 (P300) and lowest values in Segment 7 [Segments, $F(6,29) = 17.96, p < .001$].

Within-group comparisons. Because children showed much larger GFP with more variability than adults, overall analyses were also computed separately for the two groups: Children showed more GFP in the first four segments than in the last three segments [Segment, $F(6,17) = 12.46, p < .001$]. Additionally, children tended to show more GFP to symbols than to words [Wordlike, $F(1,22) = 3.56, p < .1$], which was most prominent in Segments 4 and 5 [Wordlike \times Segment, $F(6,17) = 3.81, p < .05$]. Adults showed a GFP increase from Segment 1 to Segment 4, followed by a decrease during the subsequent segments [Segment, $F(6,7) = 12.08, p < .01$]. Symbols elicited more GFP than words [Wordlike, $F(1,12) = 8.80, p < .05$], but in contrast to children, this difference was not confined to the late segments; it was present in the P1 segment, with a reversed pattern in the N1 segment [Wordlike \times Segment, $F(6,7) = 7.02, p < .05$].

Map Topography (3-D Centroids)

Between-group comparisons. Centroid distribution differed between the word and symbol conditions [Wordlike \times Polarity, $F(3,32) = 3.09, p < .05$]. Centroid mean locations of words and symbols changed differently across the seven segments [Wordlike \times Segment, $F(18,17) = 3.79, p < .01$]. Most importantly, the distinct centroid trajectories after word and symbol presentation were not the same for children and for adults [Wordlike \times Segment \times Age group \times Polarity, $F(18,17) = 3.21, p < .05$]. Furthermore, centroid mean location and distribution differed between children and adults [Location: Age group, $F(3,32) = 7.14, p < .001$; Distribution: Age group \times Polarity, $F(3,32) = 7.90, p < .001$]. These age group differences varied across the seven segments [Age group \times Segment, $F(18,17) = 4.13, p < .01$; Age group \times Segment \times Polarity, $F(18,17) = 9.33, p < .001$]. Additionally, centroid trajectories varied over the seven segments [Segment, $F(18,17) = 10.65, p < .001$; Segment \times Polarity, $F(18,17) = 227.29, p < .001$].

ERP Comparisons for Individual Segments

The Wordlike \times Segment \times Age group \times Polarity interaction indicated that specialization for letter strings was unfolding differently over time for children compared to adults, and was followed by comparisons within individual segments grouping them according to fast and slow specialization. At the segment level topographic analyses of variance (TANOVAs) were used for within-group comparisons and centroid statistics for between-group comparisons. Whereas the TANOVA on raw maps detects all systematic amplitude differences between the maps, TANOVA on normalized maps (i.e., maps scaled to unity GFP) detects only those purely topographic differences which cannot be explained by overall amplitude (GFP) differences. Both TANOVA on normalized maps and 3-D centroids are purely topographic measures, but whereas TANOVA is more sensitive to systematic differences at particular electrodes without specifying them, the centroid measures describe the differences more specifically. For GFP, separate comparisons for each age group are also reported in early components, because the much larger GFP values (means and variances) in children may otherwise have obscured condition effects in adults or in interactions. GFP and centroid analyses used repeated-measure MANOVAs as described above.

Fast Specialization for Letter Strings

P1 component (Segment 1). WITHIN-GROUP COMPARISONS. Children's word and symbol P1 maps did not significantly differ in topography (TANOVA on both normalized and raw maps; Figure 3), or in strength [GFP: Wordlike, $F(1,22) = 2.53, p = ns$]. In adults, normalized word and symbol P1 maps did not differ (Figure 3), but their raw maps differed (TANOVA: $p < .001$; Figure 3), as well as their map strength [GFP: Wordlike, $F(1,12) = 27.13, p < .001$]. These differences are also evident in the t -maps (Figure 3). Adults showed a central left-lateralized positive difference between words and symbols due to more negative values over central sites in the symbol condition (Figure 3).

BETWEEN-GROUP COMPARISONS. The P1 topography differed between children and adults according to both bootstrap comparisons ($p < .01$ for words and $p < .001$ for symbol strings) and centroids (Table 2, indicating more posterior activity in children).

N1 component (Segment 2). WITHIN-GROUP COMPARISONS. Adults' word and symbol maps differed at a high significance level (TANOVA on both normalized and raw maps, $p < .001$; Figure 3), and words elicited also

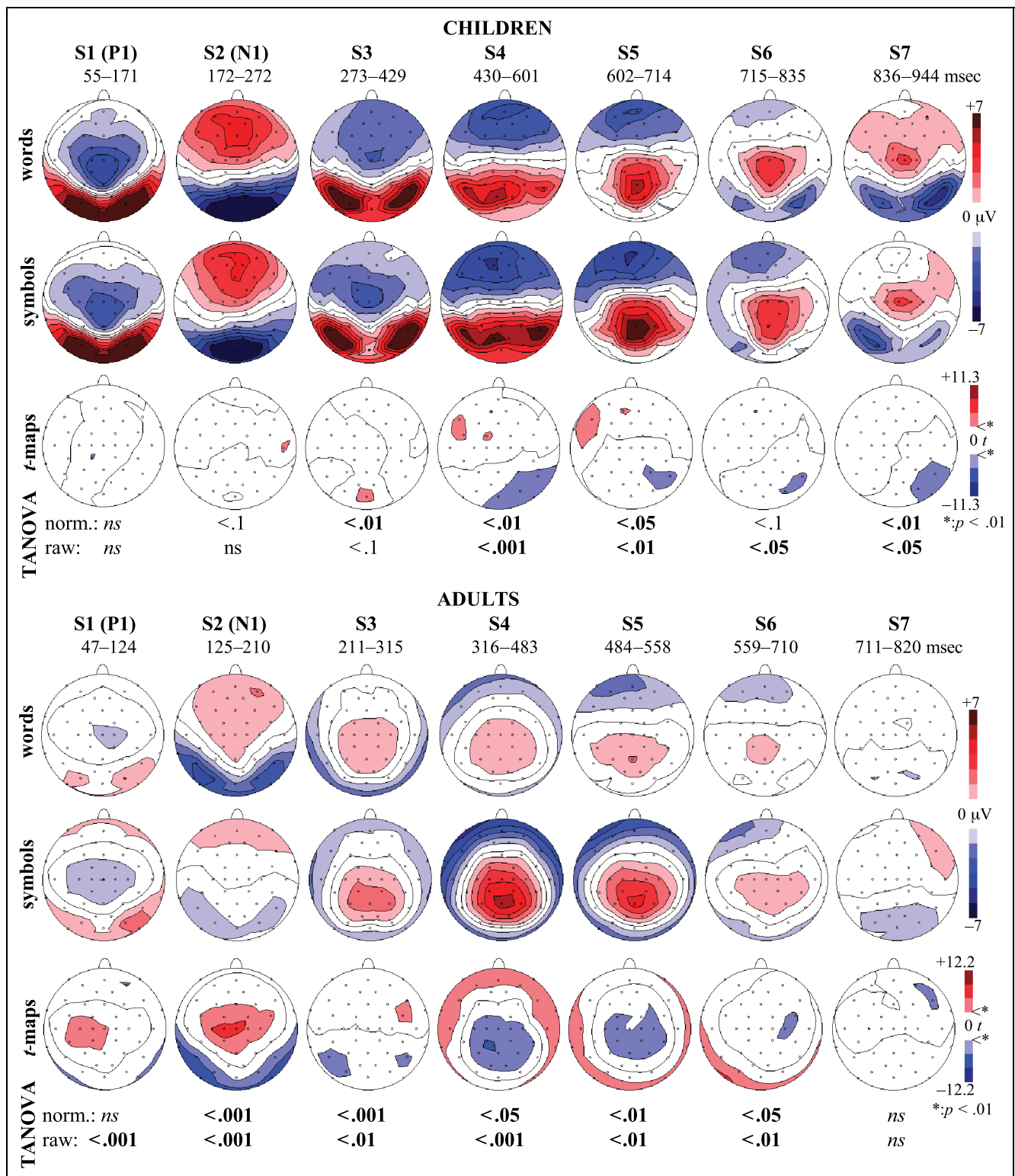


Figure 3. Segment ERP maps for words and symbol strings with t -maps and TANOVA significance levels. Maps seen from top, nose up. Note that adults, but not children, show significant word–symbol differences in the N1 segment S2. Word–symbol differences during the subsequent segments are present in both age groups, but with different topographies. Critical values in the t -maps ($p < .01$ to correct for multiple comparisons) are $t(12) = \pm 3.055$ for adults and $t(22) = \pm 2.819$ for children.

Table 2. Post Hoc Segmentwise GFP and Topography Comparisons between Word and Symbol Stimuli, Children and Adults (Significant Effects)

Segment	GFP	Topography			
		Centroid Mean Location		Centroid Distribution	
		Multivariate	Axis	Multivariate	Axis
S1	G, $F(1,34) = 94.70^{****}$ W \times G, $F(1,34) = 7.88^{***}$	G, $F(3,32) = 7.11^{****}$	y^{****}	G \times P, $F(3,32) = 3.48^{**}$	y^{****}, z^*
S2	G, $F(1,34) = 41.55^{****}$	W, $F(3,32) = 5.14^{***}$ G, $F(3,32) = 3.28^{**}$ W \times G, $F(3,32) = 3.31^{**}$	x^*, y^{****} x^*, y^*, z^* y^{***}	W \times P, $F(3,32) = 4.11^{**}$ W \times G \times P, $F(3,32) = 6.71^{***}$	y^*, z^{***} z^{****}
S3	G, $F(1,34) = 20.93^{****}$			G \times P, $F(3,32) = 45.52^{****}$ W \times G \times P, $F(3,32) = 4.94^{***}$	y^{**}, z^{****} x^{**}, y^{****}
S4-7 (averaged)	G, $F(1,34) = 35.89^{****}$ W, $F(1,34) = 27.47^{****}$	G, $F(3,32) = 6.80^{***}$	x^*, y^{**}, z^{**}	W \times P, $F(3,32) = 5.02^{***}$ W \times G \times P, $F(3,32) = 7.06^{****}$	x^{***}, z^{**} y^{**}, z^{***}

Polarity main effects have not been included in this table because they had different centroid distribution in each segment (all $p < .01$).

W = wordlike; G = age group; P = polarity; \times = interaction; x, y, z = univariate significant axis (x = left-right, y = anterior-posterior, z = superior-inferior).

* $p < .1$ (trend).

** $p < .05$.

*** $p < .01$.

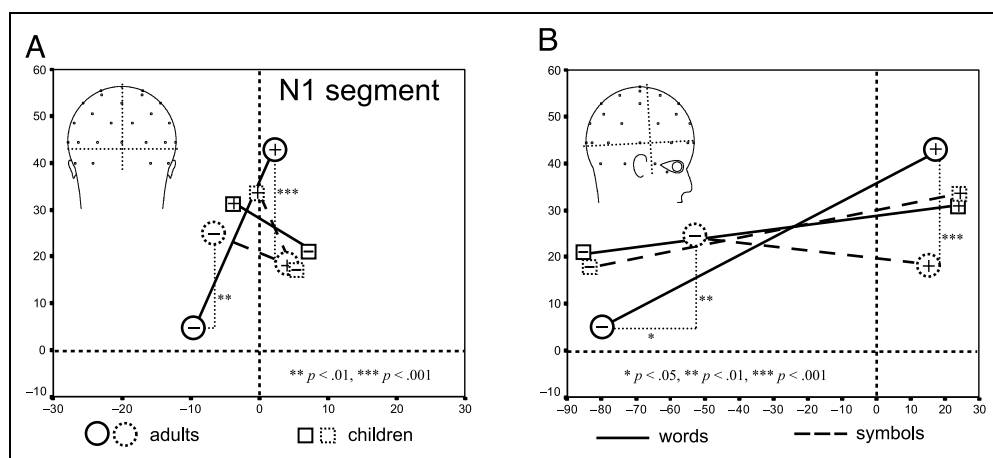
**** $p < .001$.

more GFP than symbols [Wordlike, $F(1,12) = 7.63$, $p < .05$]. In contrast, children's raw maps to words and symbols in Segment 2 (N1 component) were not different (TANOVA on raw maps, $p = ns$; Figure 3), nor were they different in overall map strength [GFP: Wordlike, $F(1,22) = 1.69$, $p = ns$], and their normalized word and symbol maps were only marginally different (TANOVA on normalized maps, $p < .1$; Figure 3). As the t -maps illustrate, word-symbol differences in adults resulted from increased occipito-temporal neg-

ativity and central positivity for words (Figure 3). Behavioral responses (differences between words and symbols in accuracy and reaction time) were not significantly correlated with GFP word-symbol difference in adults.

BETWEEN-GROUP COMPARISONS. The centroid mean location was more posterior, and tended to be more left-lateralized for words than for symbols (Table 2: Segment 2, W, x -axis and y -axis; Figure 4A). As can be inferred

Figure 4. Centroid locations after words (solid line) and symbol strings (dashed line) of adults (circles) and children (squares) in the N1 segment shown in back view (A) and right view (B). Topographic N1 word-symbol differences are indicated for adults on the z -axis for both positive and negative centroids, and on the y -axis for negative centroids (t tests). No such differences were found in children.



from Figure 4B, the mean centroid was more anterior in adults, particularly for symbols, due to more bilateral occipito-temporal, rather than occipitally focused negativities (Table 2: Segment 2, G , $p < .05$, $W \times G$, y -axis, $p < .01$). Critically, different centroid distribution for words and symbols (Table 2: Segment 2, $W \times P$, z -axis) was found in adults only (Table 2: Segment 2, $W \times G \times P$, z -axis, $p < .001$). As illustrated in Figure 4, their positive word centroid was located higher (including vertex positivity), and the negative word centroid located lower (bilateral, inferior posterior temporal negativities) than the corresponding centroids for symbols, or for the children's N1. In contrast, word and symbol centroids had a similar position on the z -axis in children. Topographic N1 differences between children and adults were reliable ($p < .001$ for both words and symbols) as confirmed by the bootstrap comparison. As for the GFP, behavioral responses were not significantly correlated with centroid location differences between words and symbols in adults.

PEAK MAPS. Planned comparisons (t -maps) at the N1 peak latency (Figure 5) corroborated the findings from the word-symbol comparison in the full N1 segment: Maps at the N1 peak (children: 223 msec, adults: 152 msec) differed strongly between words and symbols in adults but not in children. The children showed no posterior temporal differences, and isolated bitemporal differences observed in children were absent in adults. Pseudoword and word maps did not differ in either children or in adults. Although adults showed no peak N1 differences between symbol strings and pictures, prominent differences were found in children. In both children and adults, words elicited different N1 peak maps than pictures. Both symbol-picture and word-picture differences in children were mainly due to the deviant picture "N1" showing an occipito-temporal positive topography.

OCCIPITO-TEMPORAL WAVESHAPES. Planned comparisons (t -curves) at electrodes T5 and T6 (Figure 5) showed that in adults the word-symbol difference was significant (t test: $p < .01$, to correct for multiple comparisons) from about 140 to 290 msec, whereas no word-symbol differences were found during the N1 component in children. Pseudowords were not differentially processed from words during the N1 in children, and elicited only a very short differential response at about 180 msec in adults. Pictures were differentially processed from symbols in adults only at the end of the N1 component and in the subsequent component. In contrast, children's ERPs to pictures and symbols differed throughout most of the ERP including the preparatory prestimulus period. Similarly, words differed from pictures throughout most of the ERP in children. In adults, prominent

word-picture differences started near the peak of the N1.

N1 LATERALIZATION IN ADULTS. An additional analysis looked at the time course of N1 lateralization effects in adults by dividing their N1 segment into thirds. Hemispheric asymmetries at occipito-temporal sites (O1/2, PO9/10, T5/6, similar to Bentin et al., 1999) were examined using a MANOVA for repeated measures with within-subject factors "third," "wordlike," and "hemisphere" treating electrode site as multivariate dependent measures. A significant "Third \times Wordlike \times Hemisphere" interaction [$F(6,7) = 4.22$, $p < .05$] was found to modulate the expected "wordlike" effect [$F(3,10) = 29.49$, $p < .001$]. Testing each third separately revealed that negativity was more left-lateralized in words than in symbols in the two last thirds of the N1 segment [2nd third: Wordlike \times Hemisphere, $F(3,10) = 4.23$, $p < .05$; 3rd third: Wordlike \times Hemisphere, $F(3,10) = 4.01$, $p < .05$]. In contrast, this interaction was not significant in the first third of the N1 segment [Wordlike \times Hemisphere, $F(3,10) = 0.89$, $p = ns$].

Slow Specialization for Letter Strings

Segment 3. WITHIN-GROUP COMPARISONS. Segment 3 was the first segment in which children's normalized word and symbol map topographies differed significantly (TANOVA on normalized maps, $p < .01$; Figure 3). However, their raw maps differed only marginally (TANOVA on raw maps, $p < .1$; Figure 3). As illustrated by the t -maps (Figure 3), the word-symbol difference consisted of a focused posterior positivity at electrode Oz. In adults, word and symbol maps were also different (TANOVA on normalized maps, $p < .001$, and on raw maps, $p < .01$; Figure 3).

BETWEEN-GROUP COMPARISONS. Direct comparisons between children and adults revealed topographic differences in the bootstrap TANOVA ($p < .001$ for both words and symbol strings) and in the centroid analysis. In children, the positive centroids were more posterior and inferior than in adults, whereas the negative centroids were more anterior and superior (Table 2: Segment 3, $G \times P$, y - and z -axes). Positive word centroids were located further to the right in adults than in children, whereas the positive symbol centroids were located at similar positions on the right side in both age groups. Accordingly, negative word centroids were located on the left in adults and on the right in children, whereas for negative symbol centroids, the opposite pattern held (Table 2: Segment 3, $G \times W \times P$, x -axis). In adults, the positive word centroid was more anterior than the negative word centroid, whereas for the symbol centroids the opposite was true. In contrast, children's

positive centroids were more posterior than negative centroids for both stimulus conditions (Table 2: Segment 3, $G \times W \times P$, y -axis).

Segments 4–7. WITHIN-GROUP COMPARISONS. During the last four segments, word and symbol map topographies were clearly different in children (TANOVA on both normalized and raw maps, $p < .1, .05, .01, .001$; Figure 3). Word–symbol differences in children were most prominent at right occipito-temporal electrodes, where the word condition elicited less positive, or more negative values (see t -maps, Figure 3). In adults, word–symbol differences occurred also in these segments (TANOVA on both normalized and raw maps, $p < .05/.01/.001$; Figure 3), except for the last one. In contrast to the children, adults’ word–symbol differences were most prominent as a central negativity reflecting a smaller P300 for words than for symbols.

BETWEEN-GROUP COMPARISONS. For direct centroid comparison of word–symbol differences between children and adults, the last four segments (S4–S7) were averaged. The centroid distribution varied with both condition and age. For symbols, the positive centroid was right-lateralized and the negative centroid was left-lateralized, whereas words showed a reversed, less pronounced asymmetry (Table 2: averaged Segments 4–7, $W \times P$, x -axis). The positive symbol centroid was located higher, and the negative symbol centroid lower, than the corresponding word centroids (Table 2: averaged Segments 4–7, $W \times P$, z -axis). Positive centroids were always located posterior to the negative centroids; this distance was larger for words in adults but for symbols in children (Table 2: averaged Segments 4–7, $G \times W \times P$, y -axis). Positive centroids were also always located higher than negative centroids. This was more pronounced for symbols than for words in adults, but not in children (Table 2: averaged Segments 4–7, $G \times W \times P$, z -axis), and reflects the prominent symbol–P300 only observed in adults. Accuracy and speed of behavioral responses were again not correlated with centroid location differences between words and symbols in neither adults nor children. Tested separately for words and symbols, the bootstrap comparisons also indicated that topographic differences between children and adults continued (Segment 4, both $p < .001$; Segment 5, symbols $p < .001$; Segment 7, words $p < .01$, symbols $p < .05$) despite similar topographies in between (Segment 5, words; Segment 6, words and symbols).

OCCIPITO-TEMPORAL WAVESHAPES. The planned comparisons (t -curves; Figure 5) for slow effects show that in adults, the fast N1 word–symbol difference had largely resolved, and that the P300-type effects for symbol strings were not captured by these occipito-temporal electrodes. In contrast, children exhibited a prominent, longlasting, right posterior negative shift for words compared to

symbol strings between about 380 and 800 msec (t test at T6: $p < .01$; 380–800 msec). Children also exhibited additional, prominent slow differences between pictures and the other conditions.

Influence of Letter Knowledge

Although the full group of children did not show any significant signs of fast specialization for letter strings in the analysis of the global map descriptors (GFP, 3-D centroids), there was a trend in this direction both for the normalized TANOVA and for single electrodes in t -maps concerning our main hypotheses. We therefore conducted post hoc analyses to determine whether the lack of an N1 increase to letter strings in children held for those with both low and high letter knowledge, and whether letter knowledge would modulate word–symbol differences occurring after the N1. We divided the children into two groups with low letter knowledge (LL: $n = 12$, 0–11 known letters) and with high letter knowledge (HL: $n = 11$, at least 12 known letters), and ran MANOVAs on global map descriptors (GFP and 3-D centroids) for the N1 segment and the late segments including a “letter knowledge” factor. Except for letter knowledge, the two groups did not significantly differ regarding age (LL: 6.5 vs. HL: 6.6), sex (6 girls in both groups), IQ (LL: 111 vs. HL: 117), handedness (LL: 1 vs. HL: 2 left-handed), and phonological risk (LL: 1.75 vs. HL: 1.55 risk points), as revealed by t tests or chi-square tests (all $ps > .23$). We expected that the LL group would not show any fast specialization for letter strings, and that the weak signs of fast differentiation in the whole group of children (TANOVA, t -maps) would be solely due to the HL group. For the slow specialization, we had two expectations: Both groups would show a similar degree of specialization, or alternatively, the HL children would show a larger specialization.

Letter knowledge did not affect strength and topography of the late ERP segments (letter knowledge main effects and interactions in Segment 3 and Segments 4–7 were all ns for GFP and 3-D centroids). In the corresponding t -maps (Figure 6), both LL and HL children showed a right occipito-temporal negativity in their word–symbol contrast during Segments 4–7, indicating a similar degree of slow specialization for letter strings. In the N1 segment, however, the Letter knowledge \times Wordlike interactions were marginally significant ($p < .1$) for both GFP and 3-D centroids. Separate subgroup analyses revealed that GFP was indistinguishable for words and symbols in LL children ($p > .7$), but tended to be larger for words than for symbols in HL children ($p < .1$). Word and symbol centroids were also indistinguishable in LL children ($p > .4$), but differed in HL children (multivariate: $p < .05$). In HL children, the negative word centroids were right-lateralized and the positive word centroids left-lateralized, whereas the positive and negative symbol centroids were both lo-

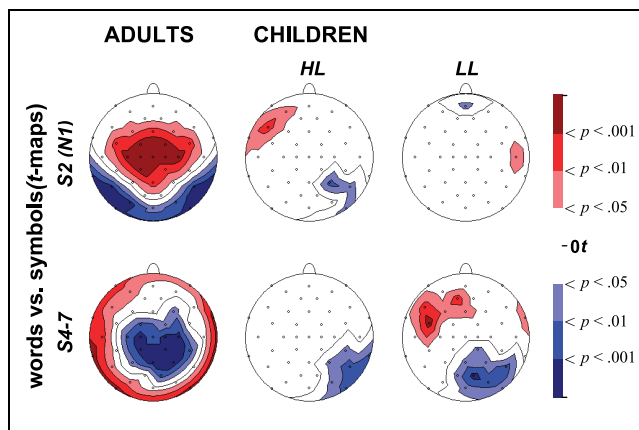


Figure 6. Fast (N1 segment) and slow (Segments 4–7, averaged) specialization for letter strings (*t*-maps of word–symbol differences) in children with high (HL) and low (LL) letter knowledge compared to adults. Only the HL children show the fast right occipito-temporal N1 word–symbol difference, which differs from the stronger and more left-lateralized N1 effect in adults. In contrast, both HL and LL children show the slow right occipito-temporal word–symbol difference.

cated slightly on the right. In the corresponding *t*-maps (Figure 6), the LL children did not show any N1 word–symbol differences. The HL children showed word–symbol differences at single right occipito-temporal and left fronto-temporal electrodes matching the lateralization in the centroid analysis. This right-occipital difference topography of HL children also contrasted with the stronger and more left-lateralized N1 difference topography in adults (Figure 6).

LORETA Source Localization

LORETA and dipole solutions for the visual P1 and N1 segments to words are illustrated in Figure 7. All source solutions were confined to visual regions. In both age groups, the solutions were more anterior and lateral for the N1 than for the P1, suggesting activation of increasingly higher visual areas over time. The opposite polarities of the P1 and N1 distributions are only reflected by the direction of the dipoles pointing towards the surface positivity. The source configurations for children’s and adults’ P1 maps were similar. For the N1, however, both symmetric occipital, and left-lateralized basal posterior temporal sources were seen in adults, whereas right posterior temporal sources were dominant in children. The extended word N1 sources in adults had a prominent left-lateralized maximum localizing within 1 cm of the “visual word form” area.

DISCUSSION

The core question of this ERP mapping study was whether nonreading kindergarten children, who had

partial letter knowledge and were visually familiar with printed words, showed signs of fast specialization for letter strings (i.e., words and other letter strings). To this end, we used an implicit reading test, and focused on comparing the children’s word and symbol string processing with data from skilled adult readers. Results demonstrated that the visual N1 in nonreading children did not differentiate between letter and symbol strings as in adults. Furthermore, letter knowledge was associated with a weak word-specific N1 response that nonetheless did not resemble the adult state. An additional precursor state of specialization for letter strings was found in late ERP segments, even in children with low letter knowledge, and might be due to visual familiarity with letter strings.

The electrophysiological data revealed large maturational effects. Children had stronger maps with different

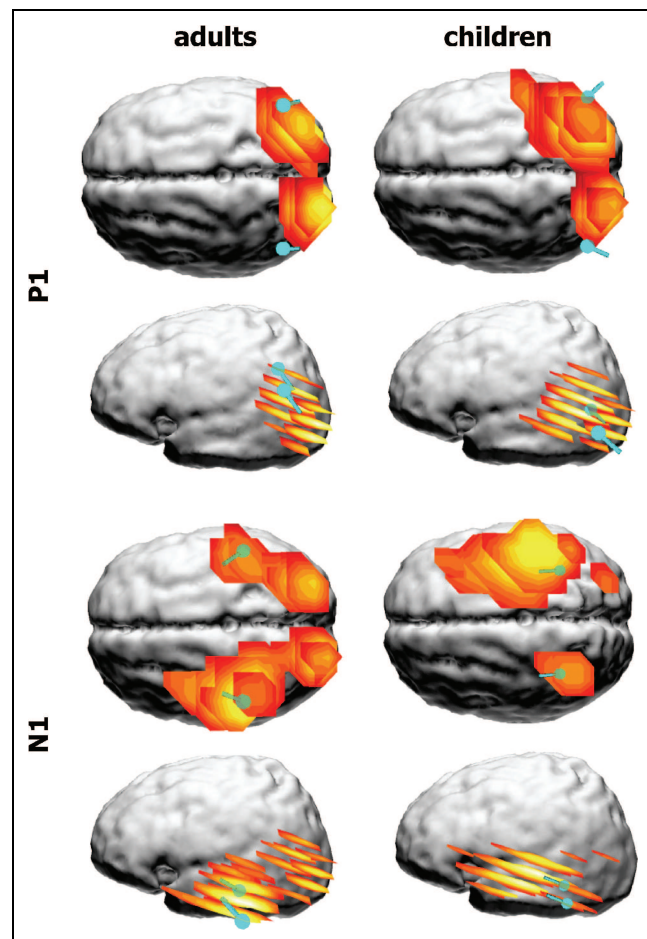


Figure 7. LORETA sources (on slices) and mirror-symmetric dipoles (cyan) using a realistic head model (from top and from the left) for the word P1 and N1 in adults and children. The distributed source clusters reveal visual activation progressing from posterior (P1) to more anterior visual regions (N1) in both age groups. A left-lateralized basal posterior temporal source cluster near the visual word form area in the left fusiform gyrus is only found for the adults’ N1. The dipole in the left hemisphere is located nearby.

topographies than adults, and longer latencies of corresponding GFP peaks and troughs resulting in later segment borders across both conditions. This is in agreement with other developmental studies reporting larger amplitudes, longer latencies, and different topographies for children than for adults (Grossi et al., 2001; Taylor & Keenan, 1999; Taylor & Smith, 1995; Holcomb et al., 1992; Kok & Roijakkers, 1985). These general developmental ERP effects are probably due to continuing maturation of the brain during childhood, such as brain growth and changes in cortical gray matter thickness (Sowell et al., 2004). Such general brain maturation should affect all N1 components equally. Instead, the divergence in the N1 between letter and symbol strings revealed a prominent specialization for letter strings.

In adult readers, words and symbol strings elicited clearly different N1 maps. Words produced increased bilateral inferior occipito-temporal negativity and central positivity compared to symbol strings. This specialization generalized to pseudowords, suggesting fast specialization for letter strings. It was highly significant and fully developed at the N1 peak latency of 152 msec, and lasted beyond the N1 segment (130–270 msec at posterior temporal electrodes). The topographic differences between letter and symbol string maps indicate different distributions of the underlying sources, consistent with activation of additional, specialized visual regions by letter strings. This fast letter-string-specific activation replicates other neurophysiological studies relating the N1 component to specialized fast visual word processing in explicit (Tarkiainen et al., 1999; Allison, McCarthy, Nobre, Puce, & Belger, 1994) and implicit reading (Brem et al., 2005; Bentin et al., 1999; Schendan et al., 1998).

In contrast, the kindergarten children's N1 maps to words and symbol strings were not significantly different using the same criteria. Their N1 maps were also larger and had a different topography than in adults. A post hoc letter knowledge analysis was performed because although the children showed no significant N1 word–symbol differences, trends were found at right occipito-temporal electrodes and for the normalized maps (bootstrap). Accordingly, the N1 word–symbol difference was marginally modulated by letter knowledge. In fact, only the children with low letter knowledge did not show any N1 word–symbol difference. The children with high letter knowledge showed marginal N1 word–symbol differences in map strength and lateralization due to larger N1 amplitudes for words than for symbols over right occipito-temporal sites, which contrasts with the topography of the N1 word–symbol effect in adults. Thus, children with low letter knowledge showed no ERP evidence for fast, specialized processing of letter strings, although they already had some letter knowledge and probably considerable visual familiarity with letters and words. The right occipito-temporal difference

in children with high letter knowledge indicates that fast and automatized processing of letter strings already starts to develop given a critical degree of early literacy, but still differs from the mature, more left-lateralized topographic difference in adults.

These results suggest that intensive reading training is necessary for the development of mature, specialized and fast processing of letter strings as found in adults. During reading instruction children learn to relate phonemes to graphemes, while they are exposed to letters and words extensively. Thus, this specialization could reflect the integration of visual and auditory processing (Molholm, Ritter, Javitt, & Foxe, 2004), or alternatively, entirely visual expertise (Rossion, Gauthier, et al., 2002; Tanaka & Curran, 2001) with letter strings. Such specialization could develop soon after the reading instruction begins, or could develop gradually through automatization of reading ability during the school years. At least part of such specialization may develop quickly, as novice readers show left-lateralized inferior-temporal fMRI activation for word processing (Gaillard et al., 2003). However, future ERP studies must clarify whether mature occipito-temporal N1 topographies specialized for letter strings develop before age 11 (Brandeis et al., 1994).

The adults' N1 was characterized by bilateral occipito-temporal negativity which was more left-lateralized for words than for symbols, consistent with Bentin et al. (1999). The absence of such lateralization in adults during the initial part of the N1 segment also agrees with previous work (Khateb, Michel, et al., 2001; Cohen, Dehaene, et al., 2000). Children also had a prominent N1, but with a more medial, symmetric occipital negativity for both stimulus conditions. This strongly suggests that the adult N1 topography is shaped along with its specialization for letter strings through late plasticity during reading acquisition, consistent with a shift from medial posterior to more lateral and anterior sources.

LORETA source clusters and dipoles in the realistic head model revealed N1 activation for adults' word processing in the inferior posterior temporal cortex with its maximum in the vicinity of the left fusiform gyrus. These solutions are in good agreement with MEG (Tarkiainen et al., 1999; Salmelin et al., 1996) and ERP (Rossion, Joyce, et al., 2003) studies finding sources for word stimuli for the equivalent time segment in the inferior occipito-temporal cortex, predominantly in the left hemisphere. Similarly, fMRI studies located word-related activity in the left fusiform gyrus (Cohen, Lehericy, et al., 2002; Polk et al., 2002; Cohen, Dehaene, et al., 2000). On the other hand, the extended source solutions also suggest that activation was essentially bilateral, and included more extrastriate occipital and more medial and superior temporal activations, similar to previous tomographic N1 source localizations (Vitacco et al., 2002; Michel et al., 2001). Because such extended

bilateral visual areas beyond the left fusiform gyrus were also activated in an fMRI study using a similar task (Tagamets et al., 2000), they might also contribute to the N1 component. Further work with more accurate source modeling based on the individual MRI, and possibly with simultaneous fMRI, should clarify this issue.

In our study, neither adults nor children processed pseudowords differently than words in the N1 segment. This confirms that the adult N1 is more sensitive to orthographic than lexical or semantic contrasts during implicit reading (Bentin et al., 1999; Schendan et al., 1998). It also suggests that the children's N1 does not reflect whole word familiarity or iconographic processes. Although the adults' N1 was very similar for symbols and pictures, children showed a massive N1 difference. Furthermore, the N1 difference between words and pictures paralleled the word–symbol difference in adults, but the symbol–picture difference in children. Both differences in children were mainly due to their occipitally strongly positive picture “N1,” which resembled a P1 topography. Such a prominent development of the picture N1 clearly indicates that reorganization of visual processing during childhood is not limited to letter strings. In children, pictures also elicited much larger P1 and P2 components than the other three conditions. This suggests that a large, sustained posterior positive activity may have overlapped with the N1 negativity in this condition. Because typical N1 distributions in response to such line drawings are found in adults (similar to Khateb, Michel, et al., 2001; Schendan et al., 1998), unmatched visual stimulus properties (larger pictures with more contours) are unlikely to be responsible. Instead, the posterior positive picture “N1” may be specific to picture processing in children. This interpretation is supported by studies reporting large developmental differences of posterior temporal activity between preschool children and adults during picture processing (Taylor, Edmonds, et al., 2001; Taylor, McCarthy, Saliba, & Degiovanni, 1999). These studies also clarify that an adult N1 topography to pictures and faces develops only after age 13 (Taylor, Edmonds, et al., 2001; Taylor, McCarthy, et al., 1999), although infants already show a negative-going posterior temporal response specific to human faces between 200 and 300 msec (de Haan et al., 2002). This suggests that activation patterns in the N1 time range may reflect the development of visual expertise and specialization without mature N1 topographies (de Haan et al., 2002). Alternatively, visual specialization may first appear as an independent ERP effect modulating later components, and may only come to dominate the N1 time range after further consolidation and automatization.

Children's word and symbol maps differed in segments subsequent to the N1. The prominent right occipito-temporal negative word–symbol difference

lasted for four topographically distinct segments (over 500 msec). In contrast to the N1 segment, this robust, slow specialization was not modulated by letter knowledge. The topography of the maps and the focal posterior word–symbol differences in the children's late ERP segments suggest that they were due to visual processing differences, possibly induced by the limited letter knowledge or by visual familiarity with letter strings. The adults' maps also differentiated words and symbols in the remaining segments—except for the final one—but their difference maps did not resemble those of the children. This slow visual precursor of literacy may reflect a right hemispheric involvement in learning to read, as suggested by Licht, Kok, Bakker, and Bouma (1986). Involvement of the right hemisphere in learning to read was also suggested by a developmental fMRI study where activation in the right inferotemporal cortex decreased with improved reading performance (Turkeltaub et al., 2003).

Behaviorally, adults proved to be more accurate than children. As expected, this difference was particularly large for letter string targets, because only adults could read. Although the task did not require explicit reading, the adults probably coded the words more efficiently at a higher (orthographic) level. In contrast, the children missed word and symbol targets equally often, indicating a lack of a more efficient strategy to process words (reading).

The children's slightly longer reaction time for words compared to symbols may suggest that limited letter knowledge or visual familiarity with letter strings led to additional processing, which would be in agreement with the differential word–symbol processing in the late ERP segments. Performance on pseudowords and words was similar, and picture targets were more accurately detected than symbols. This held for both adults and children, suggesting that neither of them could take advantage of lexical or semantic strategies in the word condition. The behavioral advantage for pictures over words was confined to children and confirms that they could not yet code words as efficiently as adults. The findings also suggest the absence of iconographic word recognition in children, although such strategies cannot be completely excluded given their tendency for longer reaction times with pseudowords than words.

In the ERP data, adults' word and symbol maps already differed at the level of the P1 component in their raw maps, but not in their normalized topography. The P1 is known to be sensitive to basic visual stimulus properties such as word or character size, or string length (e.g., Hauk & Pulvermüller, 2004; Tarkiainen et al., 1999). Because word and symbol string stimuli were matched for these features, we do not believe that differences in basic stimulus properties are responsible for this early word–symbol difference. Instead, this difference might reflect a very early stage of specialized orthographic processing, as reported in some earlier

studies (Schendan et al., 1998; Skrandies, 1998; Nobre & McCarthy, 1994). Alternatively, the blockwise presentation with fixed intervals could have led to increased preparation, reflected by larger GFP to symbols than to words. This would be consistent with the increased error rate for symbols compared to words in adults, reflecting a harder task, and a larger P300 component (associated with more perceptual resource allocation; Isreal, Chesney, Wickens, & Donchin, 1980) for symbols than for words. In contrast, the children did not show a difference between word and symbol processing in the P1 component, and missed word and symbol targets equally often. Although no word–symbol difference was found in the averaged P1 maps, their T6 waveshape showed a difference during the initial part of the P1, possibly due to residual differences in low-level visual features.

In conclusion, kindergarten children's N1 component had a distinct, immature topography. It did not yet reflect any fast specialization for letter strings in children with low letter knowledge, but indicated some immature specialization in children with high letter knowledge. The findings demonstrate the massive plasticity reflected by the N1. They also provide the first evidence that fast, specialized visual processing of letter strings does not emerge before learning to read, and that its precursor is coupled to letter knowledge. Although the results leave open at which exact age and reading level the mature N1 specialization emerges, the later ERP segments following the N1 indicate that even with low letter knowledge the kindergarten children already differentiated words from symbols. These late differences may reflect a distinct visual precursor stage of word reading.

METHODS

Participants

Kindergarten children without familial risk for dyslexia ($n = 29$, mean \pm SD , years = 6.5 ± 0.38 , 15 boys and 14 girls, 4 left-handed) and healthy adults ($n = 13$, mean \pm SD , years = 26.5 ± 3.30 , 7 men and 6 women, 2 left-handed) participated in this study. In Switzerland, children do not receive early literacy instruction in kindergarten, and reading instruction starts with school at age 7. Children and their families were contacted in their kindergartens through handouts, explaining that early readers and those not speaking (Swiss) German at home were excluded. All parents signed an informed consent form explaining the study and stating that the child is free to leave the study at any time and for any reasons. All kindergarten children were tested for intelligence (CFT-1; Weiss & Osterland, 1997), phonological abilities (BISC; Jansen, Mannhaupt, Marx, & Skowronek, 1999), early literacy (letter and word reading abilities), and visual and auditory acuity. About one and a half

weeks (mean = 11.4, range = 4–55 days) later, their ERPs were recorded.

Two children with a phonological risk for dyslexia (BISC risk points >3) and four children who could already read (more than 1 of the 9 test words read) were excluded from statistical analysis. The remaining 23 children (11 boys, 12 girls) could name an average of 11 uppercase letters ($SD = 6.5$), but could not read words, except for two children who read one word each (1 uppercase word, 1 well-known trademark label). All children had an IQ above 85 points (mean \pm $SD = 107.6 \pm 14.5$). All participants had normal or corrected-to-normal vision and hearing as tested.

Procedure

Participants were seated in a video-controlled, electrically shielded, soundproof, and airconditioned recording room 1.2 m away from the computer screen. The visual word and form processing experiment was one of seven short experiments. The experiments were presented in pseudorandom order. Electrode positions were measured with a 3-D digitizer. As compensation, each child received a small present after the study. The entire session lasted about 3.5 hours.

Stimuli and Task

The word, pseudoword, symbol, and picture stimuli were shown in black on a white background in the center of the screen. The 72 stimuli per condition were shown in two blocks of 36 stimuli containing 17% immediate repetitions serving as targets in the behavioral task. The block sequence was counterbalanced (2×4 blocks). The participants were asked to press a mouse button with their preferred hand after an immediate stimulus repetition. The stimulus duration was 700 msec followed by a 1350-msec interstimulus interval (ISI).

Words, pseudowords, and symbol strings were matched for character size (including ascenders and descenders), font size, and string length, and extended 3.3 to 7.5 cm (1.6° to 3.6°). Words and pseudowords were in lowercase letters starting with an uppercase, the common appearance of nouns in German. Words consisted of high-frequency concrete nouns from first-grade textbooks, whereas pseudowords consisted of pronounceable nonsense words (Brem et al., 2005). Pictures were drawn from the Snodgrass pictures (Snodgrass & Vanderwart, 1980). Word and symbol stimuli are shown in Figure 1.

ERP Recording and Processing

The ERPs were recorded at 500 Hz/channel with filter settings 0.1–70 Hz and with calibrated technical zero

baselines. Caps (Easy Cap, FMS, Munich) were used for the 43-channel montage, which included all 10–20 system electrodes, plus Fpz (recording reference), Oz, FT9/10, FC5/6, TP9/10, CP5/6, PO9/10, AF1/2, FC1/2, C1/2, CP1/2, PO1/2, and two EOG electrodes below the outer canthus of each eye. O1/2 and Fp1/2 were placed 2 cm more laterally for more even coverage. Impedance was kept below 20 k Ω (Ferree, Luu, Russell, & Tucker, 2001). The continuous EEG was transformed to the average reference (Lehmann & Skrandies, 1980) for all subsequent analyses. Blinks, horizontal eye movements, and in some cases, slow-wave artifacts were corrected with an advanced method which minimizes topographic EEG distortions (multiple source eye-correction method; Berg & Scherg, 1994). Corrected files were digitally lowpass filtered (30 Hz, 48 dB/oct), downsampled to 256 Hz, and segmented (–125 msec prior and 1125 msec following the stimulus). Trials with artifacts exceeding ± 100 μ V in any channel (1 adult ± 40 μ V, 2 children ± 125 μ V) were automatically rejected before averaging nontarget stimuli separately for each condition.

Grand averages were computed for each age group and condition. Adaptive segmentation used the GFP minima, which mark topographic transitions as segment borders (Brandeis, van Leeuwen, et al., 1998; van Leeuwen et al., 1998; Brandeis, Vitacco, et al., 1994), and was done separately for children (time range 0–1000 msec) and adults (time range 0–850 msec) because of the shorter latencies in adults. The GFP minima were determined in the smoothed GFP (filter = 20 Hz) of the grand mean (averaged over words and symbol condition means). Additional minima in the smoothed GFP of the separate word and symbol means were also taken into account. If two minima occurred less than 50 msec apart, the more prominent one was used. The maps in each segment were averaged. For each segment, GFP and 3-dimensional (3-D) location for positive and negative centroids (center of gravity) were separately computed at the individual level for word and symbol conditions (Brandeis, Vitacco, et al., 1994; Lehmann, 1990). GFP measures the electric field strength, whereas the 3-D centroids defined in Talairach coordinates (Talairach & Tournoux, 1988) summarize the topography of the field.

For the word–symbol string comparison, overall analyses examined global indicators of map strength (GFP) and map topography (3-D centroids). GFP was analyzed in a MANOVA (procedure GLM) for repeated measures with within-subject factors “segment” (7 segments) and “wordlike” (words vs. symbols) and between-subject factor “age group” (children vs. adults). The 3-D centroids were analyzed in a similar MANOVA, but with the additional factor “polarity” (positive vs. negative centroid). The three centroid coordinates (x -, y -, and z -axes) were treated as multivariate dependent measures. For the subsequent “segment” analyses of differences between word and symbol maps of each age group and

between the age groups, additional topographic bootstrapping tests were used (TANOVA; Pascual-Marqui, Lehmann, et al., 1999; Strik et al., 1998). TANOVA computes the exact probability of dissimilarity between two maps (Lehmann & Skrandies, 1980) using bootstrapping statistics, and protects against possible errors due to parametric statistics or nonrepresentative summary measures. Although the TANOVA on raw maps detects all systematic amplitude differences between the maps, TANOVA on normalized maps (i.e., maps scaled to unity GFP) detects only those purely topographic differences which cannot be explained by overall amplitude (GFP) differences. In direct comparisons between age groups in specific segments, 3-D centroids were analyzed using MANOVA for repeated measures as described above. For the “segment” MANOVAs, the last four segments were averaged.

In addition to this comprehensive hierarchical analysis, planned comparisons using t tests looked at the N1 peak maps and the posterior temporal waveshapes (T5/6) for differences between words and symbol strings, as well as between words and pseudowords, between symbol strings and pictures, and between words and pictures separately for each age group. The significance level was set to .05, but trends ($p < .1$) of specific theoretical interest are also reported. For all t -curves and t -maps, the significance level was set to .01 to correct for multiple comparisons.

Source localization with LORETA (Pascual-Marqui, Lehmann, et al., 1999; Pascual-Marqui, Michel, & Lehmann, 1994) was computed for the first two segments (P1 and N1) of the children’s and adults’ word grand mean data. LORETA computes the smoothest possible 3-D distributed current source density solution, which is constrained to gray matter and which produces the measured scalp map. This distributed source solution does not need an a priori number of hypothesized generators, and produces a unique but blurred solution of focal sources due to the smoothness constraint. Results are illustrated in Talairach space (Talairach & Tournoux, 1988). All solutions were computed within a realistic boundary element head model (CURRY-software; Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002; Fuchs, Wagner, & Kastner, 2001), along with a constrained two-dipole solution assuming mirror-symmetric location and orientation. Although inverse solutions are model-dependent estimates, the realistic head model used here has been shown to allow accurate estimation of inferior temporal sources (Fuchs, Kastner, et al., 2002).

Behavioral data (accuracy and reaction time) were analyzed by computing two MANOVAs for repeated measures with the factors “wordlike” (words vs. symbols) and “age group” (children vs. adults). Additionally, using t tests differences between word and pseudoword, between symbol and picture, and between word and picture conditions were analyzed separately for each age

group. Two children who missed all targets in one condition were excluded from reaction time analysis involving these conditions. Accuracy was analyzed after an arc sine transformation.

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Note

1. The term N1 is used in the present article for the occipito-temporal negative and centrally positive microstates (topographically stable segments within the map sequence) or components which directly follow the occipitally positive P1 or P100 components. Typical peak latencies of the N1 are about 150–180 msec in adults, and up to 250 msec in children. In the literature, the N1 is sometimes also referred to by its polarity and peak latency (e.g., N150 or N170 referring to its negative pole, or P150 referring to its positive pole).

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